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A synthesis of fresh water habitat requirements and status for Atlantic salmon (*Salmo salar*) in Canada

Synthèse de la situation de l'habitat d'eau douce et des besoins du saumon atlantique (*Salmo salar*) au Canada

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FOREWORD

This document is a product from a workshop that was not conducted under the Department of Fisheries Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It is one of a number of contributions first tabled at a DFO-SARCEP (Species at Risk Committee / *Comité sur les espèces en péril*) sponsored workshop in Moncton (February 2006) to begin the development of a 'Conservation Status Report' (CSR) for Atlantic salmon. When completed in 2007, the CSR could form the basis for a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report, recovery potential assessment and recovery strategy, and most importantly, enable DFO to implement pre-emptive management measures prior to engagement in any listing process.

AVANT-PROPOS

Le présent document est issu d'un atelier qui ne faisait pas partie du processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Il fait partie des nombreuses contributions présentées au départ lors d'un atelier parrainé par le MPO-SARCEP (*Species at Risk Committee* / Comité sur les espèces en péril) à Moncton (février 2006) en vue de commencer l'élaboration d'un rapport sur la situation de la conservation du saumon atlantique. Lorsqu'il sera terminé, en 2007, ce rapport pourrait servir de base à un rapport de situation du Comité sur la situation des espèces en péril au Canada (COSEPAC), à une évaluation du potentiel de rétablissement et à un programme de rétablissement mais, avant tout, il permettra au MPO de mettre en œuvre des mesures de gestion anticipées avant même de s'engager dans un processus d'inscription.

ABSTRACT

<P>
The habitat requirements for Atlantic salmon are reviewed, summarised and presented in tabular format at the micro-, meso- and macro scale. Habitat requirements by life stage are summarized from the literature. Variation in definitions for attributes describing habitat were noted and examples of attempts to standardize definitions in accordance with other disciplines are identified. The inability to integrate habitat definitions across scales was noted and identified as an area for research. The implications of theories of habitat use on the definition of crucial habitat to maintain populations is reviewed and based on the flexibility of habitat use and spatial adjustment of habitat use in response to habitat instability, maintenance and protection of a diversity of habitat is recommended for inclusion as critical habitat.
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The availability of habitat was noted to have declined some 50% since European colonization in North America and a further 16% in Canada since 1867. Substantial declines in productive capacity were identified in association with hydro power development and acidification. On the Southern Upland of Nova Scotia productive capacity had declined some 25% by 1989 and a further 25% since then due to acid precipitation and concurrent low marine survival. Only marginal losses in the productive capacity of Atlantic salmon due to acidification have been noted in other areas in Canada.
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The habitat component of those attributes that affect the capacity to produce Atlantic salmon was also reviewed. The information reviewed suggested that there was not a concurrent decline in the availability or function of the remaining habitat associated with an identified decline in abundance of salmon in Atlantic Canada since the late 1980's.
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RÉSUMÉ

<P>
Les besoins du saumon atlantique en habitat sont examinés, résumés et présentés sous forme de tableaux à petite, moyenne et grande échelle. Les besoins à chacun des stades biologiques sont résumés à partir de la documentation. Les différences de définition des attributs servant à décrire l'habitat sont notées et des exemples d'essais de normalisation avec d'autres disciplines sont signalés. L'incapacité d'intégrer les définitions de l'habitat d'une échelle à l'autre est notée et désignée comme sujet de recherche éventuelle. Les répercussions des théories de l'utilisation de l'habitat sur la définition d'habitat essentiel au maintien des populations sont passées en revue et, selon la flexibilité de l'utilisation de l'habitat et l'adaptation spatiale en réponse à l'instabilité de l'habitat, on recommande d'inclure dans l'habitat essentiel le maintien et la protection d'une variété d'habitats.
</P><P>
On note que la disponibilité de l'habitat a diminué de quelque 50 % depuis la colonisation de l'Amérique du Nord par les Européens et de 16 % de plus au Canada depuis 1867. D'importantes baisses de capacité de production sont associées aux projets hydroélectriques et à l'acidification. Sur les hautes-terres du sud de la Nouvelle Écosse, la capacité de production a baissé d'environ 25 % depuis 1989 et de 25 % de plus en raison des pluies acides et, parallèlement, du faible taux de survie en mer. Dans les autres régions du Canada, on observe des pertes seulement marginales de la capacité de production du saumon atlantique dues à l'acidification.
</P><P>
La composante de l'habitat de tous les attributs qui influent sur la capacité de production du saumon atlantique a aussi été passée en revue. L'information examinée porte à croire qu'il n'y a pas eu de baisse de la disponibilité ou de la fonction de l'habitat restant qui serait associée à une baisse d'abondance du saumon dans la région du Canada atlantique depuis la fin des années 1980.

Introduction

Canadian Atlantic salmon populations declined by at least 75% from 1970 to 2000 (WWF, 2001). Despite closures (1985, 1992 and 2000) of Canadian net fisheries for Atlantic salmon and restrictive recreational fishing regulations since 1983, populations in many rivers continue to decline. At least 550 Canadian rivers were considered to have contained Atlantic salmon historically (ICES, 2000; WWF, 2001). This number of rivers harboring populations of salmon is likely a significant underestimate by some 25% (Caron et al. 2006) when smaller rivers in remote areas are accounted. Loss of habitat for Atlantic salmon is known to be responsible for some of the more sudden and dramatic population declines, usually but not always, associated with the construction of barriers to fish passage (Leggett, 1975, Dunfield 1986). However, more indirect and subtle effects have also been documented that cause slow chronic declines in populations. This document surveys the literature for attributes of salmon habitat that may be useful to document freshwater habitat required to support viable Atlantic salmon populations and for documented changes in the productive capacity of freshwater salmon habitat, i.e., the capacity of the total habitat of a river to produce Atlantic salmon smolts at the established conservation requirement level. This approach infers that egg to smolt survival maxima for rivers are largely dependent on habitat quality, quantity and distribution and not the local fitness or loss thereof.

Fish habitat is defined under *Section 34* of the *Fisheries Act* as "spawning grounds and nursery, rearing, food supply and migration areas on which fish depend directly or indirectly in order to carry out their life processes" and applies to "all waters in the fishing zones of Canada, all waters in the territorial sea of Canada and all internal waters of Canada". This definition is noted for its broad inclusion of habitat required to supply food and migration from one stage to another as well as direct and indirect effects and inclusion of all life stages but does not provide a means to specify, compare or evaluate habitat.

Under the terms of the *Species at Risk Act*, only "critical habitat", is mentioned and "means the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species critical habitat in the recovery strategy or in an action plan for the species". Specific description of critical habitat for the survival and recovery (using the common legal interpretation of "or" to include "and") of a listed species is a developing case and ideally habitat quantity, quality and topology (spatial distribution) is associated with a probability of persistence of a population at a specified recovery target population size and/or distribution.

Within fisheries science the definition of habitat for fish has taken on many meanings depending on the scope of the question. These definitions have grown to include physical, chemical and biological attributes necessary to support fish at the micro (centimetre resolution), meso- (metre resolution) and macro (hundreds of metres resolution) scale over a range of time necessary to complete growth to migration or maturity and reproduction (Hayes et al. 1996, Poff and Huryn 1998, Armstrong et al. 2003). Achieving this goal also requires habitat through which fish must pass from one habitat to another. These descriptions, some being more specific than others, collectively encompass the scope of the legal definition of habitat interpreted by Acts, regulations, and ultimately the judicial systems. Assigning values to variables that describe attributes that enable habitat to be defined, compared and quantitatively evaluated could be termed the "science of habitat".

Determining variables and parameters to evaluate Atlantic salmon habitat for ecological, legal and economic reasons has been problematic. Problems generally lie in accepting a currency for habitat i.e., a way to compare and or evaluate habitat on a commonly accepted basis. In fact for ecological reasons the relative change in area or in the productive capacity (a limit for the production of biomass per unit area per unit time) of an affected habitat associated with a change in some attribute of habitat, e.g., water flow, has provided an acceptable legal measure in some jurisdictions to evaluate the effects of habitat manipulations on fish, e.g., Instream Flow Incremental Methodology (IFIM) (Bovee 1978), the Physical Habitat Simulation Model (PHABSIM) (Bovee 1982) and the River Hydraulics and Habitat Simulation Model (RHYHABSIM) (Jowett 1989). While these methods may respond well to some ecological and legal requirements they do not apply to all legal and economic evaluations. The capacity of or the contribution to production of fish for a habitat unit remains a goal of most fisheries habitat science and has proved to be a difficult task. The pursuit of this goal and the difficulties encountered in the description of habitat for Atlantic salmon are common threads in this review.

Freshwater habitat utilisation by Atlantic salmon is diverse, widely documented and the subject of substantial reviews (Bjornn and Reiser 1991, Gibson 1993, Bardonnet and Bagliniere 2000, Armstrong et al. 2002, Rosenfeld 2003). Publications report a range of habitats used by juvenile and adult salmon in freshwater fluvial, lucustrine and estuarial environments (see Appendix *i*). Often individual fish may utilise several habitat types during their freshwater residence (Erkinaro and Gibson 1997, Bremset 2000) for demographic (Saunders and Gee 1964), ecological (Morantz et al. 1987) as well as dynamic reasons (Bult et al. 1999).

Identification and quantification of freshwater habitats that support or limit salmon production in catchments are incorporated in stock assessment, environmental monitoring and protection activities and include *ad hoc* as well as regionally standardized methods at the micro, meso and macro scales depending on the requirements of the data or information. Perhaps because of this diversity, there is no standard accepted method utilised for measurement or assessment of Atlantic salmon freshwater habitat across the North Atlantic range of the species. In fact, common terms such as "run", "riffle", "pool", "bolder", "cobble", and "gravel" (Elson 1942, Allen 1951,) which may have standard definitions in geological, engineering or other physical sciences can vary between surveys and within regions. Objective methods have been postulated (e.g. Jowett 1993, Table 1, 2) but standardisation remains unresolved and seldom are these attributes metrically measured, calculated and reported in habitat surveys or summations.

However, this lack of standardisation is not always problematic because the use of survey data is generally limited to responses for site-, river-, or region-specific questions. Also, wide-area surveys are usually at the macro or meso scale and seldom based on these precise micro habitat definitions. There is a relative scarcity of published wide-area freshwater habitat surveys for Atlantic salmon. Nonetheless, there are benefits to cooperative management of a highly migratory species that utilises a common marine environment. These benefits underlay a common pursuit to develop standardised wide-area survey methods that could be economically applicable across the North Atlantic range of Atlantic salmon (Crosier 2003 et al., Chapter 5).

This document summarizes reported habitat descriptions by juvenile salmon stages across a range of attributes locations and authors (Appendix *i*). The document also discusses some of the theoretical aspects of habitat use and how these impact science and management. A summary of the status of habitat for Atlantic salmon in Canada is also reviewed.

Overview of Freshwater Habitat Diversity and Use

Highest population densities and productivities are associated with rivers that have moderate temperatures and flows (Jones 1949, Elson 1974, Gibson 2002) with no clear latitudinal gradient identified but rather a diversity of productivities and habitat use across regions (Elliot et al. 1998, Maki-Petays et al. 2002). These moderate climatic and stream gradient rivers have a prevalence of riffle, run and pool sections in lower stream orders (tributaries and smaller rivers) and are dominated by moderate sized "cobble" stones which are not present in every river. Descriptions of "moderate" are not always given and values for some attributes vary from document to document. One can only surmise that for specific physical attributes (later reviewed in this document and summarised in Appendix *i*) mid-range values were being referred and that there is an underlying commonality to terms like boulder, cobble and gravel dictated by the unifying forces of the physics of fluvial hydraulics and the natural geomorphology of the earth. Indeed, if one reviews the definitions of these terms in habitat surveys and cross-references with geological definitions this conclusion seems to hold depending on one's acceptance of deviation. While these substrate terms may have strict definitions in the geological sciences, terms describing the flow of water over substrates can vary, e.g., run, riffle rapid, pool etc. but again have inherent similarities among precise definitions.

Underlying hydraulic conditions are proposed to objectively classify pools, riffles, runs and rapids (Jowett 1993). Jowett proposes that common terms like these can be described by velocity to depth ratio and slope or gradient. Based on these definitions of habitat types and demographic, ecological and dynamic determinants, rivers may approach an optimum habitat distribution for Atlantic salmon as postulated by Poff and Huryn (1998) for northern rivers to be about 70% riffle area of a total stream area. This general optimization statement may be the result of the fit of the species to common stream habitat assemblages in northern temperate climates that are the result of natural history and applies to the general case but not all cases. Faced with atypical habitat distribution, stable populations can result from selection to local conditions, i.e., local fitness to less than optimum habitat.

The distribution and physical nature of habitat within streams in Canada is strongly influenced by "inherited glacial landscapes and active mass wasting processes" (Newbury 2000). Newbury's argument is that present geomorphologic stream structures, within Canada particularly, are emerging from larger geological patterns that distributed substrates and set original river courses based on larger hydraulic forces that are now being re-established to "new" rivers overlying the original geologic rivers. Both insufficient time and hydraulic forces have passed to stabilise these new rivers to classic hydro-geomorphology. Newbury suggests the phrase, rivers of "multiple origins typically Canadian" to explain the diversity of river geomorphology in Canada. This evolving process is one reason for the diversity in habitat, use and productivities of salmon that occupy Canadian rivers and could provide a background of expectations for habitat before local impacts are assessed and evaluated. Other than the Newbury hypothesis no methodology to provide this background was found. However, these processes are

discussed for specific larger rivers in eastern Canada, e.g., Miramichi River in New Brunswick and St. Mary's River in Nova Scotia in the geology literature (Ganong 1902, Roland 1982).
In addition to the over-riding geological effects on salmon habitat are regional effects such as land use, mining, forestry, linear development, urban development and impoundments that sometimes control habitat at the highest hierarchal scale (Bjourn and Reiser 1991, Poff and Huryn 1998). The mechanisms for these regional effects are diverse but include; flow alteration directly disrupting habitat or gradually altering habitat through diminished or exceeded fluvial processes associated with major dam construction and flow control (Bjourn and Reiser 1991, Armstrong et al. 2003), pH alteration from long term transport of atmospheric pollutants (Environment Canada 2004) or climatic warming and the effects of erratic and extreme precipitation events, e.g., Finny et al. 2000, Swansburg et al. 2004 and increased thermal and low flow stress associated with altered flows, e.g., Scruton et al. 2005.

Although, locally adapted population structure as defined by genetic profiles has developed in many rivers (Fontaine et al. 1997, McConnell et al. 1997) which can depend on atypical or "marginal" habitats that provide alternate forms of cover, e.g., macrophyte plants (Beland et al. 2004) or lacustrine habitat (O'Connell and Ash 1989) which by inference are also genetically structured, most populations are scaled by the size of the river. Habitat-driven population productivity (biomass or individuals at age, per unit area per unit time) of a river may be determined by the relative size of the catchments which is also a good indicator of the length of river (Elliott et al. 1998) and therefore habitat. Production of salmon, as indicated by recreational harvests, was noted to be proportionate to catchment size (Chadwick 1985). More precise estimates of catchment-wide production may utilise the relative distribution of habitat types within these catchments (Hankin 1984, Amiro 1993, Kocik and Ferreri 1998, Guay et al. 2000). However, the transportability of models and parameters to estimate the presence, production (either rate or population) or growth and survival of juvenile salmon based on a set of habitat variables remains unresolved across regions and local modeling is suggested as the only viable method to assess local productivity (Elliott et al. 1998).

Frequently questions concerning relative production potential of various habitat types are raised in order to prioritise management actions, whether those actions stem from engineering, i.e., impact assessment of a stream alteration or biological, i.e., yield of a particular stream or system of streams. This type of habitat classification sometimes referred to as a habitat classification gradient can lead to misunderstanding of the purpose and function of habitat. While marginal habitats may not have high fish production rates based on habitat quality measures such as substrate, flow or depth, these marginal habitats may be solely responsible for the persistence of local populations of salmon during times of ecological or environmental stress and are therefore critically important. This feature of habitat distribution is sometimes spoken of as "habitat complexity" (Gregory et al. 1991) and it's role, as well as the role each habitat unit plays in influencing population persistence (population viability) is suggested as a fundamental area of research required to further develop the concept of critical habitat (Rosenfeld 2003).

The effect of habitat on population growth (rate of population increase) and production (the size of a population) has been explored to some extent for single populations (Trzcinski et al. 2004) and to some extent for meta-population structure (Crosier et al. 2003, Chapter 6). However, explicit exploration of the effect on population persistence of

specific habitat units within populations is severely encumbered by the lack of information and complexity in the movements of individual juvenile salmon throughout their freshwater residence. It is possible that each habitat based life history strategy would have a different persistence vs. habitat profile further complicating the question of critical habitat. The complexity of this question, the lack of a complete analysis, and the necessity for critical habitat definitions for threatened or endangered populations begs the implementation of the precautionary approach that is based on the premise that the lack of scientific certainty should not be used to reject a cautious management action that treats all habitats as equal until proven otherwise. This does not mean that knowledge concerning the contribution of some specific habitats cannot be used to assess the impact of habitat change on population trajectories relative to the habitat under consideration.

Connectivity links a variety of habitats that can provide alternative shelter to detrimental environmental events that may not affect all habitats equally or these habitats provide a vital conduit to pass from one habitat to another, i.e., obligate habitat function. Some examples of commonly observed behavioural actions that rely on connectivity are movement and behavioural changes of parr from riffles to pools and lacustrine habitat during low water events (Gibson 1978, Morantz et al. 1987, Robertson et al. 2003), staging and diurnal downstream migration of smolts (Elson 1967, Thorpe et al. 1994).

Provision for local phenotypic expression of polygenic traits e.g., body morphologies, associated with variation in habitat types results in and maintains important genetic family lineages within river systems. In some cases polygenic traits which are assumed to convey genetically similar lineages that utilise these attributes have been identified within sub-populations and found to be heritable (Riddell et al. 1981a). Riddell et al. (1981b) noted the morphological difference between high gradient fast flowing tributaries of the Miramichi River and slower low gradient tributaries. They demonstrated through captive breeding and rearing that these attributes were inherited. Later genetic studies support this view of relative population differentiation by spatial segregation. (Youngson et al. 2003). While genetic fitness effects associated with habitat have been explored to some extent the application of these principles to management are not widespread because correlates between genetic fitness and habitat are not generally well researched (Rosenfeld 2003). The genetic family lineages that evolve in these habitats are variants of common morphology or life history strategies that can and do provide a background of variation that reduces the susceptibility of the population to extirpation driven by stochastic environmental events. These atypical strategies have been identified in some management plans that incorporate lucustrine habitat as well as fluvial habitat (O'Connell and Ash 1989) but seldom are clear differences in habitat use realised and incorporated in management. Recognition of the value of these habitats in the management of habitat is an evolving reality.

Habitat constraints to production

From the population modeling point of view any life history stage exposed to high mortality or low growth could constrain a population. In a review of the habitat factors that could control population dynamics Hayes et al. (1996) suggest listing habitat factors as consumable (also known as tropic factors in other studies, e.g., Poff and Huryn ,1998) and non-consumable factors. Within these categorisations they further classify factors as dynamically unaffected or dynamically affected, meaning that the number of fish may or may not affect the supply of the factor. All consumable factors have density

dependent interaction and non-consumable factors are postulated to have a density independent interaction. Habitat use by animals that is density independent can result in an ideal free distribution where the distribution of individuals across a range of resource patches of different intrinsic productivity equalizes to a net rate-of-gain per individual when competition is taken into account. When the density of these patches is exceeded then an ideal despotic distribution may develop where intra-specific competition for that resource better explains growth, survival and the habitat utilisation strategy of juvenile salmon (see Boisclair 2004 for a discussion). If this hypothesis is true, then habitat use within Atlantic salmon could be both ideal free and despotic depending on recruitment (dynamic effects) and/or environmental conditions. This dynamic resource use strategy could help explain the difficulties encountered in developing generalised habitat-use dependent production models for juvenile Atlantic salmon. In a somewhat controlled experiment to elucidate the habitat strategy of juvenile Atlantic salmon Bult et al. (1999) found that the ideal despotic theory better described the strategy utilized by juvenile salmon but that environmental conditions (temperature and discharge), in addition to density affects, altered the preferred choice of pool/riffle and run.

In light of these observations, management options that seek to maintain or develop a complexity of habitats including the production of consumable resources as well as maintaining optimum proportions of habitat within a river could be considered "best practice" for habitat management rather than options that seek to maximise "preferred" habitats.

The basis to assess the impact of habitat supply on fish population dynamics is conditioned by habitat supply and use relationships (Hayes et al. 1996). The functional nature of these relationships and the parameter values being used derives the integrated habitat and population dynamic effects of habitat alteration. Several indicators from these models can be used to assess the impact or efficacy of manipulating habitat factors. These are equilibrium points, abundance and recruitment rates (maximum production and slope at the origin) for abundant populations and surplus production (yield or lack thereof) for populations at low abundance.

The constraining effects of habitat on population dynamics has generally been interpreted to explain the compensatory nature of salmon stock and recruitment and generally freshwater habitat rather than marine habitat for Atlantic salmon has been implicated as a driver of this constraint (Netboy 1968, Chadwick 1985). However, many stages of age /size specific juvenile salmon have been shown to undergo moderate to high mortality (Hutchings and Jones 1998, Gibson 2006) and therefore the stage at which population regulation is affected could vary among populations of salmon. Consequently, documents report a range of habitat specific constraints that affect survivals that in turn could control population abundance. The more frequent are: physical constraints such as discharge controlling habitat (Bovee 1978, Heggberget 1991) , spawning substrate quality (Bagliniere et al. 2005), winter habitat (interstitial pockets) for both eggs and juvenile salmon survival (Rimmer et al. 1984, Cunjak 1988, Harwood et al. 2002), summer habitat for parr growth (Elson 1967) to holding pool frequency, quality and distribution of adult salmon (Frenette et al. 1975); biological constraints such as competition (intra and inter-specific) affecting survival at early life stages (Elliot 1989) and predation (for a review see Mather 1998); chemical constraints such as endocrine disrupters (Fairchild et al. 1999), pH (Lacroix 1985, Watt 1987) , and toxics such as DDT (Elson 1967); and physiological constraints regulated by temperature (Metcalf and Thorpe 1990, Crisp 1993, 1996). These components of habitat

are inter-related, and need to be viewed as a continuum (Hendry *et al.* 2003). Therefore, because of this range and variability determination of whether a variable of interest and a potential constraint is out of range from regional values is a rational first step before habitat alteration is considered. It is worth noting that, as is the case in all natural systems, relieving the prime constraint shifts population control to the next most influential constraint.

A review by chemical, physical categories of some habitat factors known to constrain populations follows;

Chemical

Nutrient limited production

No studies were found that directly link the concentration of carbon, nitrogen and phosphorus to the production or productivity of Atlantic salmon. However, one study noted increased salmon production in agricultural areas compared to forested areas (Hesthagen et al.. 1986). Studies have also shown that fertilisation can increase productivity of streams draining oligotropic catchments (Wilson et al. 2003) and enriched streams have been shown to recover from a catastrophic loss in production due to flooding faster than non-enriched sections (Weng et al. 2001).

pH and Acid-Neutralising Capacity

North American emissions of SO_2 increased during the industrial revolution (Environment Canada 2004) and peaked in the early 1970s. Reductions in emissions were implemented as a result of concerns about effects on human health and the environment. Approximately 60% of the wet sulfate deposition is from human activities in North America; the remaining 40% is background concentration. Of the 60% anthropogenic component, roughly 75% is from United States sources and 25% from Canadian sources.

The reduction in emissions is correspondingly reflected in both wet sulfate depositions and hydrogen ion concentrations at monitored sites. Anthropogenic sulfate deposition has decreased about one third since the mid-1980s. This has caused a large decrease in the deposition of acidifying substances. Unfortunately the reduction in atmospheric hydrogen (H^+) deposition has not resulted in a substantial decrease in lake acidity at measured sites in Nova Scotia, as only two of the lakes have shown reductions in acidity. Furthermore, reduction in acid deposition is not reflected in the acid neutralization capacity (ANC), as six sites show a worsening, and only three sites show improvement. Moreover, 15 lakes show a decrease in acid neutralizing base cation (C_b) concentrations. Calcium, a major component of (C_b), is an important element in salmon survival (DFO 2000).

At least 65 rivers in the Southern Upland region of Nova Scotia are severely affected by acidification (DFO 2000). The underlying geology of the Southern Upland is the principle reason for the vulnerability to acidification. Other areas in Atlantic Canada that are somewhat vulnerable to the effects of acid depositions are south western and north eastern Newfoundland. In these areas the critical sulphate loads exceed the capacity of the soils to balance pH and release base cations. Although there has been a reduction in sulphate emissions and depositions there has not been a corresponding increase in

pH or ANC in these areas. Furthermore, at the projected sulphate deposition rates the time for recovery of base cations in these catchments is 60 to 80 years (Clair et al. 2004).

Atlantic salmon populations continue to decline because the acidity of rivers in the Southern Upland region is not recovering with declines in sulphate deposition and marine survival of salmon remains low. Low marine survival results in populations of salmon which are dependant on habitats of higher productivity. At current low marine survival rates even non-lethal effects in low-acidified rivers place once viable populations at higher risk of extinction by lowering their productivity (Amiro 2000).

Toxicity Effects of low pH on Atlantic Salmon

Acidic rivers, particularly in Nova Scotia, have low concentrations of Ca^{++} (≤ 1 mg. L^{-1}) and high concentrations of dissolved organic carbon (5-30 mg. L^{-1}) and total dissolved aluminium (100-350 µg. L^{-1}). Dissolved organic matter, which is reflected by measurements of total dissolved organic carbon (DOC), is important because of its ability to chelate or bind to ionic forms of aluminium and form organic aluminium complexes. Organic aluminium is the dominant form of aluminium in Nova Scotia rivers (mean 88%) and inorganic aluminium concentrations are usually <50 µg. L^{-1}. It is the inorganic form of aluminium which can be toxic to fish. It has been demonstrated that aluminium is not responsible for the mortality of salmon associated with the acidification of rivers in Nova Scotia (Farmer et al. 1980, Lacroix ,1989). In the absence of free Al increased H^{+} ion concentrations coupled with the low concentrations of Ca^{++} are responsible for the mortality of salmon in acidified rivers (Wood and MacDonald 1982).

Mortality due to exposure to low pH in fresh water varies with the life stage of salmon. All freshwater stages are unaffected when pH ≥5.4. Significant mortality (19-71%) of fry occurs at a pH of about 5.0. Mortality of smolts also occurs at a pH of 5.0 but the rate is lower (1-5%). Mortality of parr and smolts is relatively great (72-100%) when pH declines to the 4.6-4.7 range. Mortality of eggs and alevins does not begin until pH declines below 4.8. Levels of pH ≤5.0 have also been shown to interfere with the smolting process and seawater adaptation.

Experimental data indicate that mortality of the various Atlantic salmon life stages increases with increasing acidity of dark-colored low-calcium water found in Nova Scotia.

Stage	pH	Ca^{++} ($mg.L^{-1}$)	Mortality (%)
Egg	4.64	0.67	54.5
Egg	4.92	0.85	22.2
Alevin	4.50	3.0	30.0
Alevin	5.10	3.0	2.0 – 5.0
Alevin	5.00	0.70	5.0 – 8.5

Fry	5.00	0.68	18.9 – 70.8
Fry	5.40	1.00	4.6 – 4.9
Fry	6.11	1.68	4.0
Parr	4.60	1.02	100
Parr	4.70	0.83	100
Parr	5.00	0.79	0
Smolt	4.58	0.58	72.0
Smolt	5.00	0.58	1.3 – 5.3
Smolt	5.46	1.00	0

Source DFO (2000)

A general interpretation of these data is that all stages are sensitive to pH less than about 5.3 and that eggs are the least sensitive stage to acidity in low calcium water. Alevin and parr stages are more sensitive than eggs and smolt and fry stages are the most sensitive stages.

Regular within-year variation in river water pH exists. The pH is low in cold weather months, rises from spring to autumn, then plunges down again to low winter values. Such variation is largely related to discharge, with pH being high and corresponding acid toxicity being lowest during the summer when flows are generally reduced.

Impacts of acidification on the production of salmon in Nova Scotia

A combination of geochemistry, local weather patterns, thin soils and low acid neutralizing capacity resulted in severe acidification of rivers in the Southern Upland region of Nova Scotia. Although juvenile salmon survival varies annually, there has been little or no evidence of a broad scale temporal trend in recovery from acidification. Atlantic salmon have a pH tolerance level between pH 5.0 – 5.4 depending on other river variables. For rivers in this pH range, there was a positive correlation between juvenile salmon abundance and pH ($p < 0.05$) and a positive correlation between fish species diversity and pH (Watt et al.. 2000).

Rivers with pH in the borderline toxicity range (pH 5.0 to 5.4) are at high risk of Atlantic salmon extirpation for several reasons. Sublethal effects at this pH range reduce feeding and growth, increase gill damage, and cause endocrine and osmoregulatory disruption; all effects associated with a reduction in the numbers of returning adult salmon (see Magee et al.. (2003) for review).

Aluminum levels increased in Southern Upland rivers from 1982 to 1996 (total aluminum increase = 0.019 mg/L, $P < 0.001$, resulting in increasing exposure to this toxic metal for juvenile salmon in these rivers (e.g., Poléo et al.. (1997)); however, very little aluminum is in a free ionic (toxic) form (about 1 μeg / L of Al^{3+}) and is not thought to be a health problem for salmon (see Watt et al.. 2000).

The status of 63 Southern Upland rivers was reported in the 1997 acid rain assessment. Of those, salmon were extirpated from 14 rivers (all pH < 4.7), populations had declined by 90% in 20 partially impacted rivers (4.7 < pH < 5.0) and acidification effects in 19

rivers were classified as either low or absent (pH > 5.1) (DFO 1996). Despite progress in reducing outputs from many acidifying emission sources, the chemical and salmon status of these rivers has not improved (Watt et al.. 2000; DFO 2002). An assessment of 65 rivers in 2000 reported that salmon were absent from 14 rivers of pH < 4.7 (Amiro, 2000), salmon populations were partially impacted in 24 (4.7 < pH < 5.0) and acidification effects in 22 rivers were low or absent (pH > 5.1). Amiro (2000) suggested that, of 47 rivers assessed, Atlantic salmon would become extirpated in 26 rivers, based on an assumption of 10% marine survival. At that survival rate, even rivers in which acidification effects were low could not support a harvestable surplus. Further, stocking of some rivers of the Southern Uplands was ineffective in maintaining viable populations (Amiro, 2000) and was discontinued for many rivers (DFO 2002).

Although acidity of Southern Upland rivers may not be at lethal levels for adult or juvenile salmon, sub lethal effects and increasing mortality after salmon leave the rivers could render populations unsustainable, particularly for rivers with pH between 5.0 and 5.4 or for rivers subjected to seasonal pulses of low pH. Rivers in the Southern Upland region of Nova Scotia continue to be of concern and are likely to continue to decline in Atlantic salmon populations. In fact an electrofishing survey of the Southern Upland rivers in 2000 indicated that about 50% of the rivers were likely devoid of juvenile salmon. Furthermore, in 2003 only trace populations of juvenile salmon were found in rivers that were classified as threatened in the 1999 prognosis.

Physical

Temperature

Temperature has been described as the most pervasive abiotic attribute controlling the production of teleost fishes in streams (Heggenes et al. 1993). Because fish are poikilotherms almost all of their vital activities or rates are controlled by temperature. The growing season for salmon has been estimated as the number of days when air temperature is greater than 5.6◦C (Power 1981) or water temperature greater than 7.0˚C (Symons 1979). Temperature and day length has been integrated into a growth index metric that is the product of the number of days where temperature exceeds the minimum times the number of daylight hours in a month (Metcalfe and Thorpe 1990).

The maximum incipient lethal temperature for salmon (the temperature at which all salmon would exit a habitat if the opportunity were available) was estimated to be 27.8◦C (Garside 1973). In fact many of the reported fish kills that were not associated with disease or some other physical event may be the result of prolonged exposure to temperature in excess of this limit, e.g., Moser River, Nova Scotia, 1937 and 1939 (Huntsman 1942).

A description of a function for productivity of juvenile salmon within this temperature window could not be found and therefore the optimum temperature regime is undetermined. Based on the cline in smolt age and the potential differences in the number of smolts produced per spawning salmon observed over the range it is entirely possible that an optimum temperature regime and therefore maximum smolt productivity limit exists for Atlantic salmon. This maximum is more likely at the middle latitudes rather than at the extremes of the range and may be confounded by the diversity of prey, predators and their abundances.

Temperature can also affect the movement of salmon. Juvenile salmon begin to migrate downstream as well as seek shelter in the interstitial spaces of the stream bed at about 9°C (Gibson 1978). Smolt migrations seem to coincide with rising temperatures in the spring of the year that are over 5° C and maximum movement has been associated with 10° C in some studies in eastern Canada (Forsythe 1968) and can continue up to 20° C. A switch from nocturnal to diurnal migration occurs below 7 and above 16°C (Thorpe et al. 1994).

Whalen et al. (1999b) found that when water temperatures were cold early in the year but discharge was high; few smolts were caught in their sampling trap and therefore were assumed to not be migrating. This they suggest indicates that that there is a hierarchy of cues for smolt migration with water temperature dominating discharge.

Discharge

Regardless of one's preference for a limiting habitat factor that is associated with regulating or controlling salmon populations in rivers, mortality and/or growth, both are affected by the amount of suitable habitat available, which is a direct function of discharge this is the underlying factor in habitat area models that rely on discharge or flow, e.g., IFIM, PHABSIM etc. While, exposure of juvenile populations to low flows may contribute to limiting production in streams, variation in flow is a normal expectation of salmonids occupying streams in a temperate climate. Atlantic salmon have been noted for their capacity to cope with this variation in flow and associated physical constraints better than some sympatric salmonids, e.g., brook trout. This adaptability and tolerance contributes to habitat separation and sometimes segregation. Juvenile salmon were noted to move from pool to riffle habitats at higher discharges (Bult et al. 1999) which is complementary to the noted preference to pools at low discharge (Morantz et al. 1987). Both citations note that movement is local rather than distant. The ability to adapt to changes in flow as well as their tolerance to high temperature enables juvenile salmon to occupy extensive sections of streams that experience variations in flow that are out of the habitat use range of some competitive sympatric species. However, the frequency, degree and duration of these low flow events has become a subject of renewed interest during this present awakening to recent climate change that has increased the frequency if not the extremity of these events. This change in frequency and intensity as well as timing of events could potentially affect survival of some or several stages and therefore affect the potential for persistence of a population. Further examination of the effects of these variations on population persistence is an important emerging area for research.

While it is widely held that adult run timing is keyed to discharge there is a paucity of information in the literature that develops this relationship. In fact Lilja and Romakkaniemi (2003) found that environmental indicators of the timing of river entery of Atlantic salmon in River Tornionjoki in Norway were rarely statistically significant and those that were significant in the original study did not hold over subsequent years. Delayed entry associated with low discharge is, on the other hand, widely observed. Observations of salmon holding in an estuary during low discharge events and their behavior in those estuaries have been reported and monitored (Stasko 1975, Brawn 1982). Therefore, under some discharge conditions adult salmon holding in the estuary, proximate to their river of origin, could be said to be occupying habitat necessary to support the population.

Geomorphologic

In respect to the hypothesis that Atlantic salmon demonstrate both ideal free and ideal despotic distribution (Boisclair 2004) depending on ecological and dynamic states as well as adaptive selection for habitat based on familial affinity and homing, a range of habitat types may be required in a river for population stability. Furthermore, because the proportionate distribution of these habitats are a function of geomorphology and fluvial processes that vary considerably across the range of the species it is unlikely that a single habitat type or definition will dominate the constraining factor for production of salmon populations across all regions. While there have been some reviews to classify habitat with respect to geomorphologic process (Netboy 1968, Elliot et al. 1998) on the macro scale no widely applied meso- or micro-habitat classification system based on geomorphology and hydraulic process has been widely accepted. The difficulties in developing habitat models based on geomorphology and hydraulic process are being overcome with the greater availability of data and analytic platforms. An example of explanatory results for the distribution of coarse substrates, thought to control winter habitat and therefore parr production, is the Coulombe-Pontbriand and Lapointe (2004) study of two mountain streams of Gaspé Québec. The density of parr was associated with boulder rich reaches in the Bonaventure River but maximum densities were not associated with the most boulder rich reaches in the Petite Cascapédia River. These studies develop the intricacies of the hydro-geomorphologic process mentioned above coupled with the ecological and dynamic habitat interactions as discussed by Bardonnet and Bagliniere (2000). The resulting complexity of the interactions of habitat and productivity can only be rationalised through research. Emerging research may one day rationalise the variety of freshwater habitat-based constraints observed and reported.

Obstructions

Obstructions both natural and manmade severely reduce the production of salmon. In general most vertical obstructions in excess of 3.4 m in height will block the upstream passage of salmon. The maximum height depends on the burst speed of the fish which is a function of body length which varies by age and therefore stock. Generally the burst speed of a salmon is 8 to 12 body lengths per second (Reiser and Peacock 1985). Ideally, a passable falls will have a plunge pool with a vertical drop and a depth of 1.25 times the height. Depending on the shape of the falls and plunge pool the maximum height can be considerably less (Powers and Orsborne 1985).

Dams with and without specific constructed fishway passage probably account for the most loss of salmon habitat in North America (Leggett 1975). Prior to the development of hydroelectric power there were extensive small mill dams and from 1815 to 1855 more than 30 mills a year were being built in the Atlantic provinces (Dunfield 1986) and by which time the decline in the numbers of salmon were being noticed. Although fish bypass legislation was introduced in some colonies as early as 1786 the rules were seldom followed. In Nova Scotia alone there was a total of 1,798 dams in 1851 when the first river wardens were appointed. In both Nova Scotia and New Brunswick surveys by Moses Perley, W.H. Venning and Captain William Chearnley documented severe habitat loss and destruction caused by dams and mill waste. Estimates made at the time indicated that 70 to 80% of the habitat for salmon was impacted. The first fishery regulations that included specifics for fish passage at dams was passed in 1865 but compliance was found to be lacking. A similar situation was occurring in "Upper Canada" at this time and by 1866 salmon in the tributaries of Lake Ontario, both in Canada and in

the United States were severely depleted and extirpated from many rivers. This situation led Samuel Wilmot to begin artificial propagation of salmon in Wilmot Creek in 1866, the first salmon hatchery in North America (Dunfield 1986).

With the development of the *Fisheries Act* shortly after confederation in Canada some habitat conditions improved but much damage to the populations was already done. Furthermore a new round of technology began in the late 1920's to develop hydroelectricity. This technology involved the construction of high-head dams that flooded vast areas of rivers. Fish passage structures, when required, proved to be difficult to operate effectively and in many cases were eventually abandoned for the lack of fish. Many of the major rivers were developed for hydroelectric power over the next forty years and more salmon populations were lost. Because hydro developments were naturally attracted to existing falls not all hydroelectric power developments were the direct cause for the loss of the a salmon population. No complete inventory of dams and habitat loss was found in the literature. However, it is notable that five of the largest rivers in Nova Scotia, that had salmon prior to European colonisation, were developed for hydropower and no longer have indigenous salmon populations.

Sedimentation and Siltation

Infiltration of sediment into stream bottoms has been suggested as a cause for significant decrease in the survival, emergence and over-wintering success of Atlantic salmon juveniles (Chapman 1988). Sediments size and migration in a stream (bedload) is a natural process and the natural activity of redd (egg nest) construction prepares a location such that the expected normal bedload will not significantly affect survival to emergence. However, a multitude of impacts can increase the input of sediments to streams that exceed the capacity of the hydraulic process to migrate and sort substrates; for a description of these processes and their impacts see Meehan (ed. 1991) and Chapman (1988). The result of these increased inputs of sediments is that stream substrates become embedded to the point that any stage of juvenile rearing that requires interstitial space (between the rocks) is negatively impacted. Because all but the oldest of juvenile salmon require interstitial occupation at some stage and/or environmental condition, exceeding the equilibrium input of sediments into streams can have devastating effects on the viability of salmon populations.

The first stage affected, and perhaps the most sensitive, is eggs in redds. As little as 0.02% silt has been shown to decrease the survival to the pre-eyed stage by 10% (Julien and Bergeron 2006). Survival to the eyed stage has been shown to be sensitive to a little as 0.03 -0.041% silt. Emergence survival is also sensitive to the bedload transport of sand that prevents the escapement of alevins from the gravel pockets to free swimming fry. Local stream geology, substrate distribution and resulting hydraulics act to vary these impacts throughout a stream and result in the wide range of impacts of these events and causes of juvenile mortality reported in the literature.

Habitat quantity and quality

The number of Atlantic salmon rivers in eastern Canada is not precisely known. Aside from the presence and absence of Atlantic salmon in rivers for natural and anthropogenic reasons, a part of the variation in the number of rivers is the definition of what constitutes a river, i.e., minimum drainage area, length, width, discharge or location of its discharge in fresh or marine waters. Further complicating this definition is the fact

that salmon are inherent colonisers and during times of relative high abundance and moderate climatic conditions salmon may occupy relatively small streams. This characteristic of salmon populations suggests that there is the probability that a marginal stream, from the size and discharge stability point of view, could support salmon during a high population period.

Several publications refer to a total number of rivers and some list those rivers by regions, (WWF 2001) and Salmon Fishing Areas used for management purposes (O'Connell et al. 1997). The Status of Wild Atlantic salmon: a river by river assessment (WWF 2001) lists 550 rivers in Canada. The Provincial Task Force Report (DFO 1986) lists some 622 rivers in Eastern Canada. The coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic reports a total of 646 rivers in Canada (Croizer et al. 2003). A total of 404 rivers were included in a estimate of the conservation requirements for Canada (O'Connell et al. 1997).

The present level of habitat information available by river in Canada ranges from rather coarse estimates based on drainage area and habitat to drainage area ratios developed from more finely surveyed streams or rivers to complete proximate surveys of entire rivers. Complete surveys are rarely based on a standard survey methodologies. Many habitat estimates are summations of incomplete surveys. Some are adjusted up to account for un-surveyed areas. Many rely on subjective interpretation of what is salmon habitat and arbitrary qualification is used to rate habitats (O'Connell et al. 1997). In an attempt to develop scientific based conservation requirements for Atlantic salmon. Crozier et al. (2003) noted that a minimum required value was the summer wetted surface area. They also noted that ancillary covariates are required in order to account for the variance in productivities across rivers. They point out that these variables, while not necessarily identical across all areas need to be collectable using remote methods and applicable to geographic information system (GIS) based mapping. Several initiatives have been made in this field that include GIS mapping, high resolution remote data ranging from aerial photography (Amiro 1993) and digital terrain data (McGinnity and Whalen 1992, McGinnity et al. 1997, 1999, 2000). The need for verification based on proximate survey data is pervasive throughout these studies. Crozier et al. (2003) recommend a unified concerted effort to assemble the habitat information using scientifically defensible methods appropriate for the various regions and cases. These same problems, issues and conclusions apply to Canadian Atlantic salmon habitat inventories.

Habitat status

Prior to European colonisation of North America the habitat for Atlantic salmon in North America ranged from Long Island Sound to Lake Ontario in the south to Ungava Bay in Northern Quebec (Dunfield 1986). It is not precisely known how many rivers produced anadromous Atlantic salmon at that time but is widely held that tributaries of the upper St. Lawrence River did not provide sea run populations of Atlantic salmon (Carron et al. 2006) .

With the colonising of North America by European immigrants and the use of new industrial and agricultural technologies such as the construction of dams, the freshwater habitat for Atlantic salmon began to diminish. Leggett (1975) estimated that by 1850 about 50% of the Atlantic salmon habitat in eastern North America was eliminated by

dams and/or pollution associated with industrial development and agriculture. A further 25% was affected through one means or another that reduced the productive capacity. A good deal of that habitat was within the Great Lakes and likely affected non-anadromous populations of Atlantic salmon.

Watt (1989) derived estimates of the productive capacity for Atlantic salmon using estimates of accessible drainage areas and commercial catches of salmon. While the time series regression methods utilized are susceptible to bias and error from stock and recruitment effects, variable interception and fisheries effort and catchability as well as non-sationarity in natural mortality the statistically significant trend does suggest several interesting conclusions. The adjusted (for productivity) loss in productive capacity since 1870, a time after which many of the more susceptible populations were already lost, was 8% of the total Canadian Atlantic salmon productive potential that remained at the time of Confederation(1867). Habitat loss to impoundment since 1870 was 7%. Habitat loss to acidification was 3% and therefore the total loss of the productive potential was 18% since 1870. The gain of habitat productive potential was estimated at 2% and therefore the net loss was estimated at 16% since 1870. No areas were reported by Watt (1989) with which to calibrate these losses in terms of habitat units.

In the view of Elliott et al. (1998) following a review of the rivers of Eastern North America;

"most of the rivers have been modified by flow regulation and many suffer from impacts related to other anthropogenic disturbances, principally riparian forest clearing for agriculture, forestry and urban development"

and they conclude that ;

"anadromous Atlantic salmon are diverse across the species' range and have been heavily impacted by anthropogenic disturbances".

In a further study of the effect of the long term transport of acid precipitation on the production of salmon on the Southern Upland of Nova Scotia Watt (1989) estimated a 25% reduction in the production of salmon since the 1950's was attributed to pH. A model to assess the impact of acidification on Atlantic salmon (Korman et al. 1994) was applied to 65 rivers of the Southern Upland of Nova Scotia where standard habitat data derived from aerial photographs, pH and biological characteristics from directed surveys indicated that at a present marine survival rate of 5% about 85% of the rivers would extirpate (Amiro 2000). The remaining viable river populations were generally associated with local acid resistant soils.

Elson (1974) noted a grave depletion of stocks of the Northwest Miramichi river based on "recent developments in forest management, and base metal mining" and increase home-water commercial fishery exploitation caused by delayed migration resultant industrial pollution as well as distant water fishing.

Since those times development has continued in almost all salmon producing areas and with the building of the Trans Labrador Highway undisturbed habitat for Atlantic salmon in remote Labrador is becoming even more rare. The relative impact of development ranges from nil in Northern Labrador to severe in southern New Brunswick. No comprehensive summary of the amount, quality and status of Atlantic salmon freshwater

habitat is available at this time. However, there was no evidence of acute habitat loss since the 1970's or 1980's when smolt production from the freshwater habitat of North America, principally Canadian, produced smolts that led to more than 1.6 million one sea-winter and 0.9 million two sea-winter recruits to North America (ICES 2000). Furthermore, there was no evidence that an acute loss of habitat production or productivity occurred concurrent with the sudden downturn in recruitment of salmon to North America during the late 1980's to early 1990's (Chaput et al. 2004).

Rivers of the Bay of Fundy have been subject of tidal barrage dams to drain low lying flood plains for agricultural purposes from the onset of European colonization in the early 1600's (Dunfield 1986) Since the 1900's barriers have been built for transportation, hydro power, and recreation further reducing the tidal exchange and salmon production. McCallum (2001) and Koller (2002) noted over 400 tidal barrages or gates that were operational in streams that boarder the Bay of Fundy. Some of these steams were known producers of Atlantic salmon and all would have provided forage inputs for salmon in the Bay of Fundy (Wells 1999). This loss of habitat productivity, both from direct production of salmon or input to the forage base for salmon can only be taken as a net loss to the production of salmon in the Bay of Fundy. The extent and impact of this loss is not quantified.

Summary conclusions

- Due to the diversity of habitats in Canadian rivers and the plasticity of Atlantic salmon to occupy those habitats a range in optimum habitat configurations exists across the range of the species in Canada.
- Prior to 1870 as much as 50% of the habitat was lost or the populations that utilized those areas were lost. The majority of these populations and areas were in the Upper St. Lawrence and Great Lakes (Leggett 1975).
- The net loss of productive capacity by 1989 was estimated at 16% since 1870, 8% due to loss in productive capacity, 7% due to impoundment and 3% due to acidification and 2% increased from fish passage development (Watt 1989).
- While the construction of dams and resulting flooding and flow controls may be the most prolific cause for the loss of freshwater salmon habitat in Canada, an array of distant (e.g. pH) and local (industrial land use) impacts continue to effect salmon habitats in Canada. However, no substantial and significant acute loss in freshwater habitat was reported or noted in the past twenty-five years when salmon recruitment has drastically declined.
- Development of a wide area survey method to inventory freshwater salmon habitat remains a goal for Canadian as well as international salmon management.
- An up to date inventory of the status of salmon habitat in Canada is required.
- Because some populations have been declared endangered and others meet that criteria, and because habitat explicit population viability analysis requires further development and analysis declaring all remaining producing freshwater habitat a crucial for population recovery in listed areas would be precautionary.
- The potential impact of climate change on the ability of freshwater habitat to support Atlantic salmon remains a research gap.

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Table 1. Size ranges of classes of rock aggregates that are given names in the Wentworth scale (or Udden-Wentworth) used in the United States. The Krumbein *phi* (φ) scale, a modification of the Wentworth scale created by W. C. Krumbein, is a logarithmic scale computed by the equation: $\varphi = -\log_2$(grain size in mm) (Jowett 1993).

φ scale	Size range (metric)	Size range (approx. inches)	Aggregate name (Wentworth Class)	Other names
< −8	> 256 mm	> 10.1 in	Boulder	
−6 to −8	64–256 mm	2.5–10.1 in	Cobble	
−5 to −6	32–64 mm	1.26–2.5 in	Very coarse gravel	Pebble
−4 to −5	16–32 mm	0.63–1.26 in	Coarse gravel	Pebble
−3 to −4	8–16 mm	0.31–0.63 in	Medium gravel	Pebble
−2 to −3	4–8 mm	0.157–0.31 in	Fine gravel	Pebble
−1 to −2	2–4 mm	0.079–0.157 in	Very fine gravel	Granule
0 to −1	1–2 mm	0.039–0.079 in	Very coarse sand	
1 to 0	½–1 mm	0.020–0.039 in	Coarse sand	
2 to 1	¼–½ mm	0.010–0.020 in	Medium sand	
3 to 2	125–250 µm	0.0049–0.010 in	Fine sand	
4 to 3	62.5–125 µm	0.0025–0.0049 in	Very fine sand	
8 to 4	3.90625–62.5 µm	0.00015–0.0025 in	Silt	Mud
> 8	< 3.90625 µm	< 0.00015 in	Clay	Mud
>10	< 1 µm	< 0.000039 in	Colloid	Mud

In some schemes "gravel" is anything larger than sand (>2.0 mm), and includes "granule", "pebble", "cobble", and "boulder" in the above table. In this scheme, "pebble" covers the size range 4 to 64 mm (−2 to −6 φ).

Table 2. Hydraulic characteristics (means and standard deviations) of locations classified as pool, run, and riffle habitats after Jowett (1993).

Property	Pool n=187	Run n = 760	Riffle n= 165
Froude number	0.10 ±0.10	0.36 ±0.16	0.51 ±0.26
Velocity/depth ratio	0.66 ± 0.83	2.60 ±1.74	4.69 ±3.98
Velocity (m s"1)	0.20 ± 0.20	0.56 ± 0.27	0.62 ± 0.32
Slope	0.004 ± 0.005	0.008 ± 0.008	0.016 ±0.01
Depth (m)	0.39 ±0.32	0.27 ±0.18	0.17 ±0.12
Substrate size (mm)	48.5 ± 42.0	85.5 ± 56.5	82.9 ± 56.3
Relative roughness	23.0 ±44.6	6.8 ±21.2	3.5 ± 3.8

Appendix i

Life Stage: Egg

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Egg depth (cm)**
Bardonnet and Bagliniere (2000)	20-30	40-50				15-25
Moir et al. (1998)	*24.8	*53.6				
Soulsby et al. (2001)	*25.6	*51.8				
Heggberget (1991)	50	40				
Warner (1963)			83% gravel, 16-17% sand			*20.3

Life Stage: Alevin (Fry) (6 to 7 months post-egg deposit)

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Morantz et al. (1987)	20-40	5 to 10				
deGraf and Bain (1986)		10 to 30	gravel			
Girard et al.. (2004)	20 to 39	6 to 48	pebble			
Gries and Juanes (1998)	18 to 82	*20.6+/- 1.1		pebble (47%), Cobble (39%), Gravel (8%), boulder (9%)	cobble (62%), boulder (39%)	riffle-run (58%), pool (42%)
Kennedy and Strange (1982)	<20cm preferred					riffle

Life Stage: Fry (8-12 months post-egg deposit)

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Armstrong et al.. (2003)	<10					
Beland and Trial (2004)	*28.9+/- 1	*24.7+/- 1.5	cobble			
Bremset and Berg (1999)	*139+/- 9	*<60				
Maki-Petays et al.. (2002)	15 to 60	20 to 80	cobble to boulder			
Mitchell et al.. (1998)	*23.5 +/- 2.78	*12.5+/- 3.5	daytime - *9.22+/- 5.77cm, night - *5.77+/-4.33 cm			
Nislow et al.. (1999)		12.8				
Rimmer et al.. (1984)	24-36	summer =*16.8, autumn= <10		summer *6.6, autumn *17.8		
Morantz et al.. (1987)	20-40	5 to 10	gravel			
DeGraff and Bain (1986)		10 to 30	gravel			

Life Stage: Age 1-Parr

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Armstrong et al.. (2003)			Cobble to Boulder			
Bagliniere et al. (2005)						Riffle
Beland et al. (2004)	*35.7+/- 1.2	*22.9+/- 1.9	Gravel			Riffle
Bremset (2000)	>300	4 to 10	avoided fine substrates			Pool
Bremset and Berg (1999)	*156+/- 6.0	<60				
Bult et al. (1999)						Run
Gries and Jaunes (1998)	*52.5 +/- 3.7	*23.7 +/- 4.5		2 to 19	15 to 44	Pool (53%) and riffle-run (47%)
Guay et al. (2000)	30 to 70	60 to 75	Gravel			
Maki-Petays et al. (2002)	25 to 65	20 to 80	Cobble to Boulder			
Nislow et al. (1999)		21 to 57				
Roussel et al. (2004)	20 to 30 early winter, 60 cm late winter		boulders and rubble (20-30) early winter, large boulders >40 cm late winter			
Whalen et al. (1999)	>30	<40				
Rimmer et al. (1984)	24-36	summer *29.3, autumn <10		*<20 summer, *20.9 autumn		
Cunjak (1988)	40 to 50	38 to 46		17 to 23		
Morantz et al. (1987)	30 to 60	7 to 15	Gravel and Cobble			
Coulombe-Pontbriand and Lapointe (2004)			Boulder			

Life Stage: Age 2-Parr

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Bremset (2000)	>300	4 to 10				
Bremset and Berg (1999)	*156+/- 6	*< 60				
Guay et al.. (2000)	30 to 70	60 to 75	Gravel			
Mitchell et al.. (1998)	*20.47 +/- 3.02	*11.8 +/- 5.3				
Roussel et al.. (2004)	20 to 30 early winter, 60 cm late winter		boulders and rubble (20-30) early winter, large boulders >40 cm late winter			
Whalen et al.. (1999)	>30	<40				
Rimmer et al.. (1984)	24-36	summer 30-50, winter <10		summer 6.4, autumn 24.4		
Morantz et al.. (1987)	30 to 60	10 to 20	gravel and cobble			
Coulombe-Pontbriand and Lapointe (2004)			Boulder			

Life Stage: Age 3-Parr & <

* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Beland and Trial (2004)	*35.7 +/- 1.2	22.9 +/- 1.9	gravel		Cobble or <	
Bremset (2000)	>300	4 to 10				
Bremset and Berg (1999)	156+/- 6	< 60				
Okland et al.. (2004)	60					riffle (88%), pools (11%)
Coulombe-Pontbriand and Lapointe (2004)			Boulder			

Life Stage: Adult (Spawning Habitat)
* = mean value +/- Standard Deviation where available

	Habitat characteristic					
Reference:	**Water depth (cm)**	**Velocity (cm/sec)**	**Substrate composition**	**Home stone diameter (cm)**	**Cover stone diameter (cm)**	**Riffle, Run, Pool**
Armstrong et al.. (2003)	17 to 70		Gravel (little silt and sand)		boulders important for migrating adults	
Moir et al.. (1998)	24.8	53.6	Gravel			
Soulsby et al.. (2001)	25.6	51.8				
Heggberget (1991)	50	40	Gravel (10 cm diameter)			
Crisp and Carling (1989)		>15-20	Gravel, sand, and silt (median 20-30mm)			
Beland et al.. (1982)	39	53				
Warner (1963)			83% gravel, 16-17% sand			